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Climatic Warming and the Decline of Zooplankton in the California Current

Dean Roemmich and John McGowan

Since 1951, the biomass of macrozooplankton in waters off southern California has decreased by 80 percent. During the same period, the surface layer warmed—by more than 1.5°C in some places—and the temperature difference across the thermocline increased. Increased stratification resulted in less lifting of the thermocline by wind-driven upwelling. A shallower source of upwelled waters provided less inorganic nutrient for new biological production and hence supported a smaller zooplankton population. Continued warming could lead to further decline of zooplankton.

Zooplankton play an important role in the biological cycling of carbon and other elements in the ocean. It is important to document trends in zooplankton biomass and also to understand how changes in climate may affect plankton. In this report, we describe 43 years of observations off the California coast and show that zooplankton have declined while the surface layers of the ocean have warmed. The decline is a major perturbation in the biota of the region because macrozooplankton form a significant part of the food web, may compete with larval fish for food, and are the main diet of some birds (1) and many schooling, commercially important fish species.

Our data come from the California Cooperative Fisheries Investigations (CalCOFI), a time series of physical, chemical, and biological measurements spanning an area of ocean greater than 130,000 km² (Fig. 1) since 1951. CalCOFI lines 90 and 80 are the most heavily sampled lines in the survey. Line 90 is in the Southern California Bight and line 80 is near Point Conception. Between 1951 and 1993 there were 222 cruises in which zooplankton were sampled by towing a 0.505-mm mesh net (2) at three or more stations (typically about 10) along line 90.

The zooplankton distribution is patchy in space and time. To produce a more Gaussian distribution for subsequent averaging, following the method described in (3), we computed the natural logarithm of the plankton volume, per 1000 m³ of seawater strained, at each station. The transformed data were averaged over all stations from a given cruise along lines 90 and 80 to produce a time series for each line (Fig. 2, A and B). Zooplankton volumes decreased by about 80% from 1951 to 1993. In addition to this trend, there were low-frequency fluctuations with periods of years to decades. Because of the high interannual variability, it is uncertain whether the decline occurred gradually over the whole time series or more

rapidly since the 1970s. The zooplankton volume at line 80 was consistently higher than at line 90, characteristic of the general northward increase in plankton volume, but the interannual variability and the downward trend were similar at the two lines.

We investigated the spatial dependence of the zooplankton decline by averaging over the initial and final 7-year periods of the survey at each station location (Fig. 3). These intervals were selected because they include a large number of cruises (71 and 27, respectively) but avoid effects of strong El Niño–Southern Oscillation episodes in California waters during 1958–59 and 1983–84. The decline from the initial to the final interval was about 80%. The difference appears to be uniform in space and is at least twice the standard deviation of the 7-year mean at each station. Spatial patterns were similar during both time intervals, with zooplankton increasing northward and shoreward.

For comparison with the zooplankton decrease, we analyzed temperature, salinity, and geostrophic transport in the upper 100 m at line 90. A warming trend previously identified (4) is evident (Fig. 2C). No trend was seen in upper-layer salinity or transport, although there were substantial decadal fluctuations in salinity, including a decrease of about 0.2 practical salinity unit (psu) from 1981 to the present.

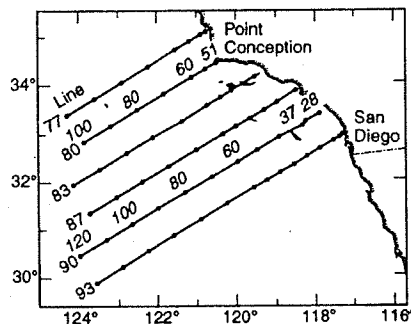


Fig. 1. CalCOFI survey plan, with station numbers (italics) indicated on lines 80 and 90.

We also averaged temperature, salinity, and geostrophic velocity over the same initial and final 7-year intervals as was done for the zooplankton data. Line 80 and line 90 surface temperatures (Fig. 4) warmed by an average of 1.2° and 1.6°C, respectively. Near Point Conception, the upwelling center for the region, surface temperature increased from 12.5° to 14.1°C between the two intervals. Temperature changes were reduced at depth, to 0.2°C at 180 m averaged along line 80 and at 270 m along line 90. As a result of the surface-intensified warming, the vertical stratification of the thermocline substantially increased and less cold waters came into contact with the atmosphere in the upwelling zones.

Salinity within the thermocline changed little between the initial and final periods. However, because of the warming, which in effect displaced isotherms downward, salinity on constant-temperature surfaces increased by up to 0.15 psu (at 10°C). Geostrophic velocity at line 90 showed an increase in the wind-driven recirculation—greater northward flow near shore and greater southward flow offshore—but no change in net transport.

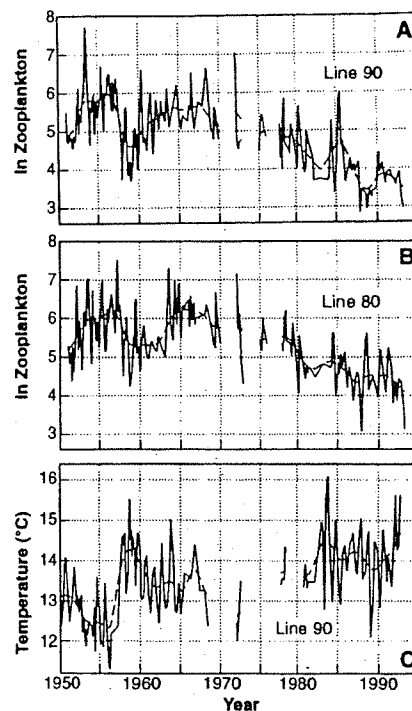


Fig. 2. Time series of log-transformed zooplankton volume (cubic centimeters of zooplankton volume per 1000 m³ of seawater strained) for (A) line 90 and (B) line 80. On the logarithmic scale, a change of -1.6—which in (A) and (B) is the change from the mean of the 1950–1970 data to the minimum in the 1990s—is equivalent to an 80% decrease. (C) Time series of the upper 100 m average temperature for line 90.

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Bakun, analyzing a combination of directly estimated winds and onshore-offshore barometric pressure differences (geostrophic wind), has suggested that coastal winds favorable to upwelling off California increased substantially from 1946 to 1988 (5). However, there are possible biases in this climatology. The directly estimated winds reported by ships at sea tend to be irregularly distributed in space and time (5), and the geostrophic estimates may also be skewed

because the upwelling zone is narrow compared to the spatially smoothed climatology. To illustrate, alongshore winds from CalCOFI stations during the period 1951 to 1993 (Fig. 5) show the narrow band of positive curl (upwelling) near shore at line 90 out to station 55, with negative curl (downwelling) farther seaward. While the reported increase in alongshore wind is consistent with the increase in oceanic recirculation noted above, its expected consequences are opposite the observed increase in temperature and decrease in zooplankton.

The observed changes in temperature and zooplankton over 43 years allow an assessment of thermal and ecological imbalances that are too small to measure instantaneously. A warming of the upper 100 m of the sea by 1°C requires a heat input of $4.3 \times 10^8 \text{ J m}^{-2}$, equivalent to only 0.3 W m^{-2} for 43 years. Although such a small residual cannot be measured in instantaneous or annually averaged heat balances, the long-term warming is robust and has had substantial effects on coastal sea level rise (4).

The observed rate of decrease in zooplankton volume is $6 \times 10^{-10} \text{ s}^{-1}$ for an 80% decline over 43 years. On long time scales, zooplankton biomass is controlled by the net effect of decreases due to excess mortality over reproduction versus increases through advection by ocean currents from the north (6). Advective input is estimated to be $\sim 5 \times 10^{-8} \text{ s}^{-1}$, far larger than the observed trend. The long-term trend thus is a small residual of much larger terms; it cannot be isolated by studies of advection, reproduction, or mortality. Nevertheless, it too is a dramatically large signal when accumulated over 43 years.

We suggest that the observed warming is linked to the zooplankton decline. As the sea surface is heated, the temperature difference across the thermocline increases,

here by about 25% between the sea surface and a depth of 200 m. For a given alongshore wind stress, the (upwelling) displacement of the thermocline is inversely proportional to stratification (7). In other words, an increase in stratification results in reduced displacement of the thermocline. With less upward displacement, shallower layers bearing fewer nutrients are exposed to light, leading to less new production and ultimately to decreases in zooplankton. The mechanism is not a decrease in the volume of upwelled waters; it is a shoaling of the source of upwelled waters. Depending on relative magnitudes, this effect of heating could offset or even reverse the effect of an increase in wind stress.

The above mechanism relates a moderate surface warming to a major decline in the biota. In the waters along line 80, the nitrate concentrations decrease from about $30 \mu\text{mol/liter}$ at 8°C to 0 at about 14°C and warmer. Upwelled waters colder than 14°C contain nitrates but upwelled waters warmer than 14°C do not, having been stripped of nitrate at the sea surface in the basin-wide band of downwelling farther offshore. The effect of a sharper thermocline, with less vertical displacement due to wind stress, is to decrease the fraction of the year when wind stress is strong enough to lift nutrient-bearing waters to the sea surface near the coast. Thus, by insulating nutrient-bearing layers from the sea surface, a moderate degree of surface heating can greatly reduce the nutrient supply.

The observed trends in the California Current may be related to basin-scale changes in wind forcing. A strengthening of the North Pacific wintertime atmospheric circulation began in the late 1970s (8), near the time when the CalCOFI trends discussed here began to be clearly seen. A number of other effects have been observed in relation to this basin-scale change (9). It is possible that a shift in ocean circulation, such as at the bifurcation of the west wind drift reaching North America (10), might

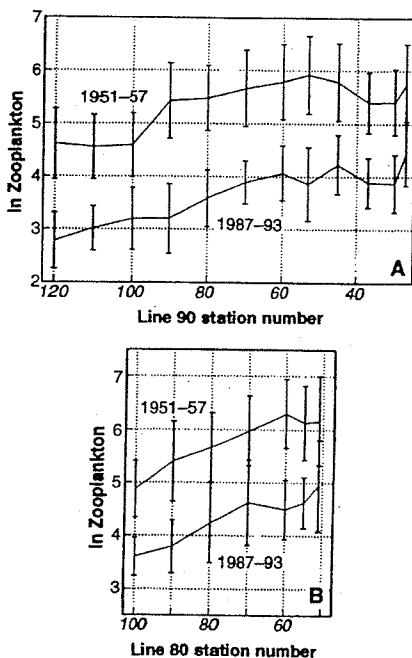


Fig. 3. Temporal average and standard deviation (vertical bars) of log-transformed zooplankton volume for all cruises during the periods 1951 to 1957 and 1987 to 1993 along (A) line 90 and (B) line 80. On this logarithmic scale, a change of -1.6 is equivalent to an 80% decrease. Station number units are equivalent to 4 nautical miles.

Fig. 4. Average temperature ($^{\circ}\text{C}$) for the periods 1951 to 1957 (A) and 1987 to 1993 (B) along line 90 (left) and line 80 (right).

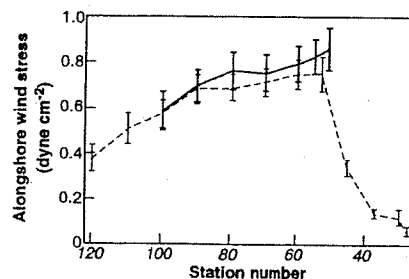
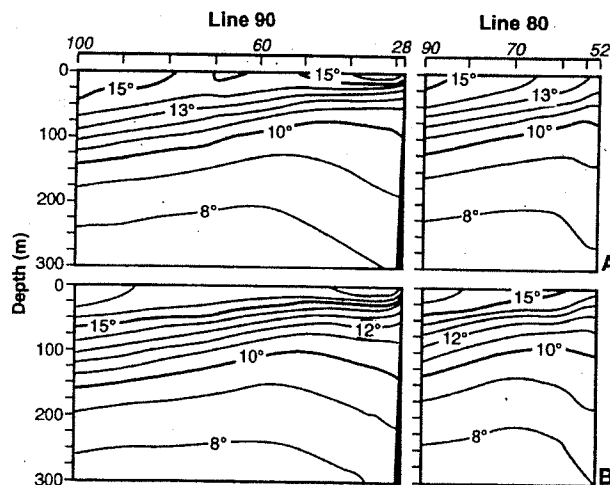


Fig. 5. Temporal mean and standard error (vertical bars) of alongshore equatorward wind stress (wind toward 150°) at CalCOFI stations along line 80 (solid) and line 90 (dashed) between 1951 and 1993, using stations with more than 80 observations.

import warmer water, decrease the supply of nutrients, or decrease the volume of zooplankton carried by the California Current.

The future consequences of the observed decline in zooplankton volume are closely tied to the question of causality. If the decline is part of a natural cycle that reverses in coming years, then any impact may be similarly transient. On the other hand, if the zooplankton decline is anthropogenic or is a natural trend of longer duration, then the large magnitude of the response is of great concern for the coastal ecosystem. The suppression of nutrient supply by enhanced stratification is not a mechanism confined to coastal oceans. If there is a global temperature rise of 1° to 2°C in the next 40 years and stratification increases globally, the biological impacts could be devastating. Our study also demonstrates that climate studies dominated by short-term process-oriented experiments cannot

simply be extrapolated to decadal time scales, where the balance of terms is different from monthly or seasonal balances.

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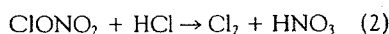
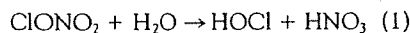
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The Reaction of ClONO₂ with Submicrometer Sulfuric Acid Aerosol

D. R. Hanson and E. R. Lovejoy*

The measured reaction probability, γ , for the reaction of chlorine nitrate (ClONO₂) with 60 percent (by weight) sulfuric acid aerosol increases monotonically with particle size at 250 kelvin. The reacto-diffusive length (ℓ , the effective liquid depth over which reaction occurs) derived from these experiments is 0.037 ± 0.007 micrometer (95 percent confidence level for precision). The reaction probability for the reaction of ClONO₂ with 60 percent sulfuric acid aerosol doped with $\sim 7 \times 10^{-4}$ M hydrochloric acid at 250 kelvin is larger by about a factor of 4 than in the absence of hydrochloric acid and varies less with particle size ($\ell = 0.009 \pm 0.005$ micrometer). These results provide a test of the theory for gas-particle reactions and further insight into the reactivity of atmospheric aerosol.

Both ClONO₂ and HCl are relatively stable, gas-phase reservoirs of Cl in the stratosphere. Mechanisms that release Cl from these reservoirs enhance O₃ destruction by accelerating the Cl catalytic destruction cycles for O₃. The following heterogeneous reactions are important mechanisms for converting reservoir species into products that are readily photolyzed and that release Cl atoms:



These reactions contribute to the winter-spring polar O₃ loss (1) and to the global destruction of O₃ during volcanic aerosol loadings (2, 3).

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Although the uptake of ClONO₂ by bulk liquid H₂SO₄ solutions has been studied extensively (4–6), the reaction probability of ClONO₂ with submicrometer H₂SO₄ aerosol is unknown, and the parameters necessary to extrapolate the bulk results to the small aerosol that is characteristic of the stratosphere are uncertain. In this report, we describe measurements of the variation of the ClONO₂ reaction probability with particle size for submicrometer-sized H₂SO₄ aerosol, with and without HCl. These results provide an unprecedented test for the theory of the kinetics of gas-particle reactions and a basis for understanding the reactivity of atmospheric aerosol.

The rate of processing of a gas-phase reactant (x) by monodisperse aerosol is given by

$$\frac{d[x]}{dt} = -\gamma c \pi r^2 [P][x] \quad (3)$$

where γ is the reaction probability, c is the mean molecular speed of x in the gas phase,

r is the particle radius, $[P]$ is the particle concentration, and $[x]$ is the concentration of x in the gas phase. For clarity, we do not discuss the small corrections for the diffusion of the gas-phase reactant to the particle (7). The reaction probability (γ) is given by

$$\frac{1}{\gamma} = \frac{1}{\alpha} + \frac{c}{4HRT\sqrt{k^1 D_\ell} \left[\coth\left(\frac{r}{\ell}\right) - \frac{\ell}{r} \right]} \quad (4)$$

where α is the accommodation coefficient (the fraction of collisions that lead to accommodation by the liquid surface), H is the effective Henry's law coefficient (ratio of the liquid-phase concentration to the gas-phase concentration at equilibrium), R is Boltzmann's constant, T is the absolute temperature, k^1 is the first-order rate coefficient for loss of x in the liquid phase, D_ℓ is the diffusion coefficient of species x in the liquid, and ℓ is the reacto-diffusive length defined as $\ell = \sqrt{D_\ell/k^1}$ (3, 8, 9). The reacto-diffusive length ℓ is the effective depth of liquid in which reaction occurs. Equation 4 demonstrates that the resistance to loss of the gas-phase species ($1/\gamma$) is the sum of the interfacial resistance ($1/\alpha$) and the reactive resistance (second term on the right side of Eq. 4). For small reaction probabilities ($\gamma \ll \alpha$), the reaction probability is given to a good approximation by

$$\gamma \approx \frac{c}{\gamma_0 \left[\coth\left(\frac{r}{\ell}\right) - \frac{\ell}{r} \right]} \quad (5)$$

where γ_0 is the bulk reaction probability.

When ℓ is small relative to the size of the particle ($\ell \ll r$), the reactant is consumed

The Center for Liquefied Natural Gas. Webpage: Newsroom>"Offshore LNG Project Impacts on Marine Life Assessed to be Minimal." Press release January 17, 2006. Viewed at <http://www.lngfacts.org/newsroom/011806.html>. Viewed May 7, 2006.

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Offshore LNG Project Impacts on Marine Life Assessed to be Minimal

Analysis Discovers Methodology Overstates Results

WASHINGTON, D.C. - The actual impact of offshore liquefied natural gas (LNG) projects on marine life in the Gulf of Mexico will be substantially less than originally identified by environmental analyses, according to findings released today by The Center for Liquefied Natural Gas (CLNG) from an independent ecological review of the analyses.

CLNG commissioned Exponent, Inc., to undertake an independent evaluation of the technical work that has been done to date in assessing environmental impacts from use of seawater in open loop vaporization (OLV) systems proposed in LNG terminals in the Gulf. The primary environmental question associated with the use of OLV technology is the potential for impact on fish eggs and larvae into seawater intakes.

The environmental impact statements (EIS) developed by the United States Coast Guard for proposed offshore LNG developments conclude that the impact on fisheries would be minor. However, some have disputed this interpretation and others have raised concern about cumulative impacts if several offshore LNG terminals are built in the same region.

"Our findings indicate that the actual impacts of offshore LNG development, and in particular the use of OLV systems, on fish populations is expected to be substantially less than the minimal impacts already predicted in the EIS," said Paul Boehm, PhD, vice president, Environmental Services, Exponent. "The EIS conclusions that impacts will be minor are indeed correct, and can be used for licensing decisions."

"The Exponent report confirms and strengthens CLNG's position on the acceptability of the use of OLV, a proven and environmentally sound technology used throughout the world," said Bill Cooper, Executive Director, CLNG. "We've learned that the current methodology uses very conservative assumptions that overstate the impacts. This is an important finding that the effects will be much smaller than initially reported."

Exponent found the EIS assessments contained numerous conservative assumptions that "significantly over-estimate the potential for adverse impacts" from offshore LNG projects. After adjusting the fish equivalent methodology used in the EIS with a more scientifically appropriate approach consistent with the National Oceanic and Atmospheric Administration (NOAA) approach for stock assessments, estimates of impacts were

significantly lowered. For example, the impact of the Gulf Landing LNG project is estimated to be equivalent to the loss of 8 mature female redfish. Even though cumulative impacts were insignificant in the EIS assessments, using the more rigorous egg equivalent method yields even smaller cumulative impacts from LNG projects in the Gulf region.

The Exponent report reaches the following major conclusions:

- OLV operations would have only minor environmental impacts
- The best available data and conservative assumptions were used in the EIS to make the determination of minor impact
- EIS to date have over-estimated the environmental impact and are inconsistent with other NOAA stock assessment models
- Cumulative environmental impacts are even less than the minor impacts predicted in the EIS

"CLNG remains confident that OLV technology can be used in an environmentally responsible manner to deliver clean-burning natural gas to meet U.S. energy needs," said Cooper.

For a PDF copy of the Exponent study, [see here](#):

Exponent, Inc. is a multidisciplinary organization of scientists, physicians, engineers, and regulatory consultants performing in-depth investigations in more than 50 technical disciplines. The company investigates and analyzes failures and accidents to determine their causes and prevention and evaluates and solves complex human health and environmental issues. Exponent is certified to ISO 9001.

CLNG is a coalition of LNG producers, shippers, terminal operators and developers, energy trade associations and natural gas consumers. Its goal is to enhance public education and understanding about LNG by serving as a clearinghouse for LNG information.

CHAPTER 4: CALIFORNIA'S OCEAN ECOSYSTEM

CALIFORNIA'S OCEAN ECOSYSTEM

Habitats within California's ocean ecosystem contain some of the most biologically diverse natural communities in the world. The abundance of species and habitats located offshore California can be attributed to the inter-relationship of the identified resource zones located both onshore and offshore. Onshore, an extensive system of inland waterways provide habitat for various marine species, as well as freshwater and nutrient flows. Offshore, several major oceanic factors, such as the California and Davidson Currents and a hydrological phenomenon known as upwelling, contribute essential nutrients to nearshore and deep ocean waters. These factors create at least three offshore regions between Mexico and Oregon which exhibit notably different biogeographical characteristics due to currents influencing temperature, nutrients, and distribution of the organisms and their offspring. It is beyond the scope of this analysis to fully identify the many factors affecting the diversity of biological resources off the California coast. However, the analysis does describe the major interactions between different ocean resource zones, how these interactions affect diversity, and the fact that modifications in one zone may strongly influence biological processes in other zones located miles away.

OCEAN RESOURCE ZONES

For descriptive purposes, the habitats which make up California's ocean ecosystem have been grouped into four geographic zones (see Figure 4-1):

- **inland watershed zone**, including all watersheds within the State that ultimately drain from their headwaters into the Pacific Ocean;
- **enclosed waters zone**, including the waters and associated terrestrial habitats of bays, estuaries, coastal wetlands and lagoons;
- **nearshore ocean zone**, including nearshore open coastal waters out to the boundary between the Continental Shelf and Continental Slope (depths range from 100 to 300 meters depending on the location); and
- **offshore ocean zone**, extending from the boundary between the Continental Slope and Continental Shelf to the edge of the exclusive economic zone (200 miles offshore).

The following sections provide examples of the habitat types, flora and fauna, and current issues that relate to each ocean resource zone. This summary is not intended to be a comprehensive accounting of the natural characteristics or issues that may arise within these zones, but rather to generally describe the inter-relationships between these zones to emphasize the need for management approaches which are responsive to the needs of the overall ocean ecosystem. Such an approach, termed ecosystem management, recognizes and responds to these inter-relationships for the benefit of all resources and species within California's ocean ecosystem, including species listed under federal or state law as threatened or endangered (see Appendix G). More detailed analyses of current issues affecting California's ocean ecosystem are provided in Chapter 5.

THE INLAND WATERSHED ZONE

California's extensive inland watershed zone consists of the watersheds surrounding the approximately 7,800 miles of rivers, creeks and drainages, traversing diverse climates, geography, and topography as they meander towards the Pacific Ocean. These watersheds play a critical role in providing freshwater flows which support anadromous fish and dependent habitats, such as coastal wetlands and nearshore

coastal waters. In addition, these watersheds provide habitat and cover, as well as transporting sediment from inland sources to the sea, providing a critical source of sand for beaches along the entire California coast.

Habitat Types

The health and productivity within California's inland watershed zone depends on the appropriate distribution of sediments, adequate vegetation along waterways, and sufficient flows of freshwater. Coniferous forests, common along northern streams and in the upper reaches of most watersheds, function to retain topsoil and prevent sediment loading in rivers. When sediment loads increase, stream channels and associated wetlands may lose their effectiveness for flood control and as wildlife habitat. Riverside forests and riparian woodlands provide nutrients, shade, and channel stability, permitting river waters to support spawning and the survival of young fish, such as salmon. Freshwater wetlands, also common to the inland watershed zone and often associated with rivers, are important for controlling and reducing the effects of peak flood flows, breaking down pollutants from contaminated waters, providing fish and wildlife habitat, and settling sediments before they reach coastal or urbanized areas. Adequate stream flow and water quality are required for anadromous fish to reach their spawning grounds, successfully spawn, rear to emigration size, and safely reach the ocean.

Flora and Fauna

Numerous fish species spend most of their lives in the ocean, but are seasonally dependent upon rivers and streams for reproduction. Known as anadromous fish, these species include the Coho and Chinook salmon, steelhead trout, American shad, striped bass and white sturgeon. Anadromous fish require rivers and associated tributaries for migratory routes, as well as for spawning and nursery grounds. Although these species historically used rivers and streams along the entire coast of California, the strongest remaining populations of anadromous fish typically occur in the rivers near and north of the San Francisco Bay. Some anadromous fish, such as the striped bass and white sturgeon, mainly spawn in the Sacramento-San Joaquin Delta.

Striped bass (an introduced species), as well as many native anadromous fish, have shown significant population declines in the last decade. For instance, the winter-run Chinook salmon in the Sacramento River has decreased in recent years from a high run of 117,808 fish in 1969 to a run of 200 adults in 1994 and 1,300 adults in 1995 (Schafer (a), pers. comm.). At least sixteen marine anadromous fish species depend on the inland watershed zone for survival at some point during their life cycles (Moyle, pers. comm.).

Current Issues

Land reclamation activities, including agriculture and urbanization, have resulted in a significant loss of the state's historic distribution of freshwater and riparian wetlands. In addition, dam construction, river channelization and water diversions have altered the natural flow of many rivers which, in combination with increased sediment loads from such activities as logging and cattle grazing, has diminished recreational and environmental values. Pollution also has become a problem with nearly 75% of the pollutants entering marine waters originating from land-based activities (Weber 1993). These pollutants ultimately find their way to coastal wetlands or nearshore ocean waters. Overall, habitat alteration, including modifications in water management regimes, increased pollutant loads, and impacts of introduced plant and animal species, has adversely affected many fish and wildlife populations dependent upon the waters of the inland watershed zone.

Looking Forward

A variety of efforts have been initiated to reverse this trend. The California Department of Fish and Game, California Department of Water Resources, and U.S. Bureau of Reclamation, have ongoing habitat restoration and fishery protection programs within the Central Valley. These projects include stream bank protection, stabilization, and re-vegetation, as well as installation of structures to provide cover, renovating scour holding and rearing pools, new and improved fish screening devices, increased stream flows, and removal of barriers to upstream migration. Two major restoration activities are currently underway in the Central Valley to help recover and maintain such anadromous fish as Chinook salmon, steelhead, striped bass and sturgeon. The congressionally-mandated Central Valley Project Improvement Act has the goal of doubling these fish populations by using some of the aforementioned measures. The CalFed Bay-Delta Program is developing a comprehensive plan for actions to restore the biological carrying capacity of the San Francisco Bay/Sacramento-San Joaquin Delta estuary as well as the many of the key streams in the watershed.

A variety of other planning efforts are in progress, such as the development of a water quality protection program for the Monterey Bay National Marine Sanctuary, which is developing strategies for watershed management reaching far into the Salinas Valley. The Coastal Conservancy is completing a number of watershed management plans on many waterways flowing to the ocean including the Klamath, Eel, Garcia, Navarro, Russian, Petaluma, Napa, Salinas, Santa Clara, Santa Ynez, Ventura, Santa Margarita and Otay Rivers and for a number of major creeks. When completed, these plans will specify restoration and enhancement projects intended to improve riparian and wetland habitats, which play such an important role in the health of California's ocean ecosystem. The California Department of Parks and Recreation has been active in watershed and habitat restoration activities on State Park System lands, including stream and river stabilization and restoration, exotic species removal, prescribed fire use, road removals, and land form restoration. The Governor's 1997-98 Budget proposes a \$3.8 million Watershed Initiative to assist the Department of Fish and Game, the State Water Resources Control Board, the Department of Conservation, and the Department of Forestry and Fire Protection in efforts to reduce water quality and habitat impacts in key watersheds throughout the State of California.

THE ENCLOSED WATERS ZONE

The enclosed waters zone is ecologically, economically, and recreationally important to California, as bays, estuaries, coastal wetlands and lagoons are the places where land meets the sea. Freshwater originating from as far away as the Sierra Nevada mixes with saltwater from the Pacific Ocean and, in the process, creates some of the State's most unique and sensitive habitats. This zone differs from the inland watershed or ocean zones because of the mixing of fresh and salt water and the substantial influence of tidal forces on the habitat. While the enclosed waters zone supports an abundant and diverse assemblage of plants and animals, it is largely dependent upon nutrient inputs from the inland watershed, nearshore ocean, and to a lesser extent, offshore ocean zones for maintenance of these organisms.

Habitat Types

Emergent coastal wetlands, mudflats, and seagrass meadows are the major habitat types present within the intertidal portions of the enclosed waters zone. These three habitats, although distinct in many ways, are strongly dependent upon one another. Transitions among these habitats are often gradual, with the same nutrients, plants and animals sometimes found in more than one habitat. For example, young fish and invertebrate species migrate between emergent wetlands and submergent seagrass meadows as tidal fluctuations submerge and expose different areas of an estuary.

Emergent coastal wetlands usually occur in intertidal marine, brackish, and freshwater areas of the enclosed waters zone. Vegetation produced in wetlands supports an extensive food chain, largely based on the consumption of decaying plant material by organisms known as detritivores. Although vegetation

production in wetlands may be high, the diversity of vegetation species is low due to difficult conditions created by salinity and fluctuating water levels. Ecologically connected to coastal wetlands, upland areas within the inland watershed zone are a refuge for many creatures from rising tides and raging storms.

Mudflats, composed of soft, fine sediments, are another common habitat in the enclosed waters zone, occurring in intertidal areas. Mudflats form in areas where impacts from ocean wave activity is low and water movement is minimal. These conditions create a gentle slope that is much flatter than that observed for sandy beaches. These gentle slopes, coupled with fine sediment particles, result in long water retention, in turn allowing organic material to accumulate and serve as an abundant food source for the creatures residing in mudflats.

Submerged seagrass meadows are another prominent habitat in the enclosed waters zone and often occur in the shallow subtidal areas. Dense seagrass beds, in conjunction with emergent wetlands, perform many important functions, such as providing fish and wildlife habitat, reducing coastal erosion, and filtering pollutants from the water column before they can flow into the Pacific Ocean. Soft bottom channels and submerged seagrass beds often provide a transition between the enclosed waters and nearshore ocean zones. These habitats are less conspicuous than others in this zone because they are frequently covered by water and, therefore, usually not seen by the casual observer. Tidal scour and freshwater flushing create highly changing sediment and salinity conditions, and are the driving force in the formation of seagrass beds and soft bottom channels. Currents in the channels can reach velocities of up to several knots, creating soft bottom areas where organisms must be highly adapted for survival. Tidal conditions in submerged seagrass beds are diminished, allowing sediment to settle and seagrasses and other organisms to flourish. Although conditions in the subtidal habitat can be severe, anadromous fish and other organisms have adapted to and use the habitat as migratory channels and feeding grounds.

Flora and Fauna

The high productivity of plants and algae in the enclosed waters zone attracts large numbers of animals. For instance, habitat provided by the stems and roots of emergent wetland and submerged seagrass vegetation provides spawning, nursery, and feeding grounds for important fishery species, such as the striped bass, California halibut, white sea bass, herring, and various salmonids. Taller wetland plants, such as the cordgrasses and bulrushes, provide cover and nesting sites for the endangered light-footed clapper rail, while shorter vegetation provides habitat for the endangered Belding's savannah sparrow. Other prominent coastal birds, such as the snowy egret, great blue heron, and endangered least tern, are common to wetland and seagrass habitats, while eelgrass (the dominant seagrass species in the enclosed waters zone) is the primary food source for the black brant, a migratory goose. This region also provides important habitat for other species including amphibians, reptiles, and mammals, some of which have been listed as either threatened or endangered (see Appendix G).

The apparently barren appearance of mudflats is deceiving. Organic material carried into mudflats via tidal action is decomposed by microscopic bacteria which play a vital role in recycling food for other organisms. Bacteria are very abundant in mudflats, with populations of hundreds of million per gram of sediment. Nutrients made available by bacteria support algae, including diatoms and blue-green algae which can form mats up to one centimeter thick. Sediments provide habitat for large populations of commercially valuable invertebrate species, such as clams and oysters, as well as non-harvested species such as other mollusks, crustaceans, and worms. Staghorn sculpin, starry flounder, leopard shark, and California skate are common fish in mudflats. Mudflats also provide foraging areas for many coastal birds, including the long-billed curlew, marbled godwit, snowy plover, and gulls.

Current Issues

Evidence suggests that many bays, estuaries, coastal wetlands and lagoons have been substantially altered or eliminated in California. Historically, ninety percent of emergent wetland habitats and more than half the mudflats in the enclosed waters zone have disappeared, while substantial levels of seagrass meadows

have been lost. Most of this loss is the result of physical displacement from coastal developments, or the result of modifications to other resource zones which eliminate the supply of fresh and salt water to these areas. (Dennis and Marcus 1984).

For instance, hydrological changes in a watershed drainage may adversely reduce or increase the supply of water or nutrients to distant coastal wetlands and seagrass meadows. These changes can also increase sediment loads and runoff, causing adverse effects to watershed ecosystems that include smothering flora and fauna, increased streambank erosion, and increased turbidity. Water quality degradation from polluted runoff generated within inland watersheds and from point sources can affect resources such as shellfish beds and nursery habitats for various species of fish. Events that sometimes occur offshore, such as oil spills that reach bay, estuarine, and wetland habitats, can have devastating effects on resources within the enclosed waters zone. Other activities that impact this zone include dredging and filling activity to maintain harbor channels and entrances, as well as increasing instances of non-native species being transported into California ports from ships discharging foreign ballast water. Many introduced plant and animal species are reproducing in large numbers and competing with native species.

In addition, sea level rise is a phenomenon that may significantly affect the enclosed waters zone. For example, research conducted in the San Francisco Bay Area indicates that, over the last 120 years, the sea level at Golden Gate Bridge has risen an average of about 2 millimeters per year or about 9.5 inches total (Conomos, et al 1985). There are predictions that global warming may cause the sea level to rise another 2 to 3 feet in the next several decades. If this occurs, there will be dramatic changes in the shoreline and dynamics of the enclosed waters of the San Francisco Bay/Sacramento-San Joaquin Delta system, the largest estuary in California.

Looking Forward

Although some wetland losses continue, the conversion of major wetlands and other resources within the enclosed waters zone has been largely abated, and properly designed and monitored mitigation projects are being conducted to increase such habitats. Habitat restoration and mitigation projects, either planned or ongoing, are being pursued for many coastal wetlands throughout the State, consistent with the Governor's 1993 wetlands conservation policy which calls for no overall net loss of wetlands, and for achieving a long-term gain in the quantity, quality, and permanence of wetland acreage and values. For example, the Sonoma Baylands, Elkhorn Slough, Cargill Baylands, Ballona Wetlands, and Batiquitos Wetlands projects are intended to result in substantial increases in the quantity and quality of habitat values in those areas.

Regional planning efforts will be important in restoring and/or enhancing resources within the enclosed coastal waters zone. Regional wetlands planning is essential to the success of implementing the Governor's wetlands conservation policy. The plan implementing that policy calls specifically for three geographically-based regional strategies, including the San Francisco Bay Area and Southern California.

In the San Francisco Bay Area there are many concurrent wetlands planning and protection efforts underway. These efforts were called for both in the Governor's policy and the San Francisco Estuary Project's Comprehensive Conservation and Management Plan. Many of these efforts are based on cooperative outreach with landowners and other stakeholders. A program designed to develop regional wetlands goals is currently being undertaken by the Regional Wetlands Ecosystem Goals Project (a coalition of government, the private sector, and academia). This group is working to provide a common basis for identifying important wetlands resources, setting future restoration and enhancement goals, and working together to improve the decision making process.

In Southern California, the Governor's plan calls for the development of a joint venture project to set wetlands restoration and enhancement goals. This process has not yet been formally instituted; however, a coastal wetlands inventory has recently been initiated by the State Coastal Conservancy, California Coastal Commission, and U.S. Fish and Wildlife Service. Additional data may be gathered to address the

important coastal watershed wetlands resources. There are a number of coastal wetland restoration projects either underway or being proposed for Southern California area.

Lastly, the complicated issue of introduced or exotic species to the State's bays, estuaries, coastal wetlands, lagoons and adjacent lands must be addressed. These species have been invading California's ocean ecosystem, particularly within and around San Francisco Bay, resulting in substantial environmental and economic damage, including the destruction of wooden pier structures and the crowding out of many native species of ecological importance. The California Department of Parks and Recreation has been active in removing exotic species, as well as in dune stabilization and re-vegetation, on California parklands. The California Department of Water Resources also spends considerable resources on studying and removing harmful exotic species. New measures may be necessary at the State, federal, and international levels to develop ballast water discharge procedures that will reduce the introduction of waterborne exotic species into California waters.

THE NEARSHORE OCEAN ZONE

The nearshore ocean zone extends from such onshore areas as sandy beaches, boulder fields and rocky outcroppings, including associated kelp beds, sandy and muddy bottoms, to the boundary between the continental shelf and continental slope (depths range from 100 to 300 meters, depending on the location). Waters of this zone are rich in nutrients primarily from upwelling currents and partially from freshwater inflows, supporting an abundance of habitats and organisms which also offer many economic and recreational opportunities.

Productive oceanographic factors, such as major ocean currents, stimulate biological productivity and diversity in both nearshore and offshore ocean waters. The California Current is a cold water current that originates north of California and moves southward along the coast, whereas the Davidson Current is a periodic, nearshore current that flows in a northerly direction, carrying warm waters from semitropical seas to Southern California. Another factor is upwelling, the movement of deep ocean waters into shallower, nearshore areas. Upwelling provides essential nutrients needed to support vast populations of microscopic organisms collectively known as plankton. Plankton are a vital component of numerous food webs supporting important fish, mammal and bird populations.

Interactions between offshore currents influence temperature, nutrients, and distribution of organisms and their offspring and create three distinct marine biogeographical regions (or bioregions) along the coast of California. The southern region, extending from the Mexican border to Point Conception near the City of Santa Barbara (known as the Southern California Bight), is composed of warmer waters and primarily supports temperate and warm water fish and invertebrate species. Point Conception is a transition zone where warmer Southern California waters mix with colder waters from the north. The second region is located offshore the Central and Northern California coast, extending from Point Conception to Cape Mendocino where another transition zone occurs. A third region, extending from Cape Mendocino beyond the California/Oregon border (sometimes known as the Oregonian Province), contains colder waters and organisms adapted to such conditions. (Cailliet and Greene, pers. comm.). These distinctions are important, because they play a major role in explaining offshore conditions and differences in species distribution along the coast.

Habitat Types

Wave action exerts a strong influence on habitat distribution within the nearshore ocean zone. Fine, sandy beaches often occur in areas where wave action is light, while beaches with more coarse sand are found where wave activity is stronger. Sandy beaches are dynamic habitats in which sediments are constantly shifted down the coast and between deeper and shallower waters. Waterways in the inland watershed zone play an important role in this process because they transport sediments that ultimately provide sand for the State's beaches. Boulder fields occur in areas of greater wave activity, and rocky outcroppings

occur where wave action is the greatest. The pounding surf within boulder fields and rocky shores often creates small habitats known as tidepools, which support creatures uniquely adapted for survival under such extreme physical conditions as temperature variation, salinity, and wave action. Although shoreline habitats may appear distinct from those offshore, they are dependent upon each other, with the exchange of nutrients and organisms among them being common.

Kelp forests, shale, and sandy and muddy bottoms are the dominant habitat types occurring just offshore.

Kelp forests are common in areas with rocky substrates and may extend for miles along the coast, forming habitats that, in some ways, function similarly to terrestrial forests. Species may be found at different depths within kelp forests, which grow in water depths up to 100 feet. Some organisms prefer the anchor-like holdfasts near bottom sediments, others prefer the stem-like stipes in the mid-water column, and still others mostly inhabit upper canopy areas near the ocean's surface. Shale, also known as hard bottom, occurs in the nearshore ocean zone as a substrate for burrowing organisms.

Sandy and muddy bottoms are common along the entire coast of California. Sandy bottoms are located intermittently along the coast, while muddy bottoms are most common at the mouths of rivers and estuaries, where sediment loads of silt and clay settle out as the water moves further offshore.

Flora and Fauna

California's nearshore ocean zone is rich in biodiversity and commercially important species. Giant kelp, common to many coastal regions, is the largest and fastest growing algae in the ocean. While kelp forests provide refuge and forage areas for many sea creatures, they are also harvested regularly for use in manufactured products, such as cosmetics and ice cream. Commercial and recreational fishing have a long history in California's nearshore ocean zone. Some species with current commercial value include the sea urchin, squid, abalone, spiny lobster, California halibut, Pacific mackerel, rockfish, and several species of crab. Commercial importance can vary over time; for example, in just over 20 years, the red sea urchin has risen from virtual obscurity to become California's largest grossing single-species fishery.

Many vertebrates, including fish, birds and mammals, also are common in the nearshore ocean zone. The sandy beaches of Southern California serve as the major spawning grounds for grunion, which wriggle onto beaches during certain full moons to mate and lay eggs. Rockfish, white seabass, lingcod and various perch species are common to kelp forests, while white croaker, halibut and other flatfishes often inhabit muddy and sandy bottoms. Shorebirds, such as sandpipers, godwits and curlews frequent sandy and muddy shores, where they feed on tiny invertebrates buried beneath the sand. Other bird species, including many gulls, the endangered California least tern, the threatened brown pelican, and the snowy plover, nest and feed within this zone. Many of these species can be particularly sensitive to disturbance.

Several mammal species depend on nearshore ocean habitats for forage and breeding grounds. Harbor seals, sea lions and elephant seals are among the pinnipeds commonly seen along the coast of California. San Miguel Island, located in the Santa Barbara Channel Islands National Marine Sanctuary, is estimated to support the largest concentration of pinnipeds in the world. The California sea otter, a threatened species, occurs locally along the central coast of California, usually in association with kelp forests and sea urchin colonies. Once numbering less than 100, the sea otter population in California has risen to approximately 2300 individuals. Whales and dolphins swim into nearshore waters, but these species are more common in deeper, offshore waters.

Current Issues

Throughout the world, coastal areas tend to support large human populations. A problem associated with increasing populations is coastal development and increased pollution. Discharge of pollutants from point sources, such as sewage and industrial wastes, is monitored closely in California although the appropriate level of treatment continues to be controversial. Another problem of an international nature is that Mexico's discharge regulations are less strict, which has resulted in some increased pollution levels in the

waters offshore San Diego. Waters of the nearshore ocean zone also receive pollution from such sources as agriculture and urban run-off from watersheds in the inland watershed zone. In addition to increased water pollution, dredging and filling that accompany coastal construction and development have significantly affected the ecological functioning of many nearshore areas. Comprehensive monitoring programs for nonpoint sources of pollution have not yet been established.

Discharge and intake systems from coastal desalination facilities, coastal power generating stations, and waste treatment facilities (discharges only) all affect California's nearshore ocean zone. Issues arising from these operations include fish and larval entrainment from intake systems and potential adverse impacts to kelp, fish, other marine species, and humans from coastal discharges. Oil spills, both on and offshore can also cause substantial adverse impacts to resources within the nearshore ocean zone. Numerous government and private sector efforts are moving forward to reduce these impacts.

In the 1800's, many species of marine mammals which live in the nearshore ocean zone were hunted to near extinction for their fur, meat, and oil. However, enactment of the federal Marine Mammal Protection Act of 1972 now protects these creatures, and many populations have grown significantly in recent years. The population of northern elephant seals, for instance, was once reduced to less than 100 individuals by hunting and now numbers approximately 80,000 in California. California sea lions now number approximately 160,000 along the California coast, with an average annual population increase of about 8 percent (Schultze, pers. comm.). In fact, some of marine mammals are at or above historic levels and are beginning to occupy habitat not previously used. This has resulted in some inevitable conflicts with humans, which are likely to increase as marine mammal populations continue to expand. Recovery of these species is due in part to cooperative efforts of California's commercial fishers and fishery managers to dramatically reduce the take of marine mammals such as sea otters, harbor seals, and sea lions in fishing gear in recent years. However, the take of some species of whales is occurring in certain fisheries at a level that is inconsistent with the provisions of the Marine Mammal Protection Act. Therefore, particular efforts are being initiated to seek reductions in the take of these species from some drift gill net fisheries.

Some coastal fishery stocks have declined, resulting from a combination of factors such as habitat disruption, changing ocean conditions, and overfishing. Funding limitations have significantly reduced the ability of most State and federal agencies to implement necessary resource assessment and habitat restoration efforts or to fully enforce existing fishery management laws and regulations to help identify changes and, where necessary, reduce the decline of fishery stocks.

Looking Forward

A variety of efforts to identify and control sources of nonpoint pollution are underway by several departments within the Resources Agency and the California Environmental Protection Agency. However, ongoing and potentially expanded water quality maintenance and monitoring programs will be essential to ensure that water quality standards are being met. Interaction between growing populations of marine mammals and humans is an issue that must receive more attention in the future. Some species, such as elephant seals, are hauling out and breeding on mainland sites for the first time ever. In some cases these breeding grounds are moving toward popular beaches frequented by recreational users which creates potential hazards for both humans and elephant seals. Competition between marine mammals and both sport and commercial fisherman for fishing grounds is another concern which may have to be addressed in the future. While management guidelines have been formulated for most important fisheries in California, comprehensive management is conducted for only a few, such as northern anchovy, Pacific sardine, and Pacific herring.

THE OFFSHORE OCEAN ZONE

The offshore ocean zone of California begins at the boundary between the continental shelf and continental slope and extends to the edge of the exclusive economic zone (200 miles offshore). The exceptions to this

general definition are deep submarine canyons which split the shelf in some areas and bring the deep ocean environment in close proximity to shore. For example, the Monterey Submarine Canyon in Central California reaches a depth of nearly two miles and approaches within 300 feet of the beach. This diversity of depths, combined with a strong connection to the ecology of both upland habitats and deep ocean waters, creates an environment vital for supporting a diverse biological community and significant economic, recreational, and educational opportunities.

Productive oceanographic factors stimulate biological productivity and diversity in both nearshore and offshore ocean waters. These factors include the California Current, periodic Davidson Current, and the phenomena known as upwelling, which provides essential nutrients needed to support vast populations of plankton. Plankton are a vital component of numerous food webs that support important fish, mammal and bird populations. Three biogeographical regions (or bioregions) are created by these factors: 1) Mexico to Point Conception, known as the Southern California Bight; 2) Point Conception to Cape Mendocino; and 3) Cape Mendocino north into Oregon, known as the Oregonian Province. These regions are discussed in greater detail in the nearshore ocean zone description.

Habitat Types

The habitats of this zone are generally identified as an upper area where sunlight is sufficient to support primary productivity, a middle transitional area where sunlight is weak and not supportive of primary productivity, and a lower area completely beyond the influence of sunlight. Another habitat is often identified as the surface of the ocean which supports birds and other species which require both air and water to survive. Each of these habitats has a unique ecology with characteristic plants and animals (or lack thereof). In general, temperature, oxygen, atmospheric pressure, and nutrients combine to restrict many species to specific depths. On the other hand, there are many species that use more than one habitat area during their life cycle or even on a daily basis. For example, anchovies most frequently school in commercial quantities near the surface, but at certain times of year they are known to school at depths greater than 200 meters during the day and near the surface at night. Also, while bottom-dwelling animals may never leave their deep ocean realm as adults, their eggs and larva can often be found in the transitional or upper habitat areas.

Flora and Fauna

In the relatively shallow waters of the offshore ocean zone, there is an abundance of plankton. Phytoplankton directly harness the power of the sun through photosynthesis, while zooplankton feed upon the phytoplankton. Small and abundant, plankton form the base of many food chains and support such commercial fisheries as herring, mackerel and sardine. In addition to being consumed by small fish, plankton also support shrimp-like crustaceans known as krill, the major source of nutrition for the largest creatures on earth, including blue and fin whales. The offshore ocean zone also supports other important fishery stocks typically restricted to deeper waters, including tuna, swordfish, rockfish, sablefish, Pacific hake and flatfishes.

The abundant food sources in the offshore ocean zone also support other vertebrate populations, including numerous bird and marine mammal species. Several large birds, such as albatrosses, frigatebirds and various gulls, travel many miles from shore into the offshore ocean zone to feed on crustaceans and small fishes. California sea lions and northern elephant seals also travel far out to sea in search of fish and other food sources. Although blue and fin whales are now relatively uncommon in the offshore zone, other marine mammals are commonly found in California's offshore waters, including gray and humpback whales and several species of dolphins and porpoises.

Current Issues

Similar to other natural areas in California, the offshore ocean zone and its inhabitants are facing increasing pressures from human activities. Dredge disposal, oil and gas operations, shipping operations, military

exercises, seismic testing, or sound experiments in the water column can disturb or potentially harm marine life within this zone. For instance, change in the historical migratory patterns of gray whales along California's coast has been associated with shipping activity and increased noise pollution, while overfishing and nearshore habitat degradation may be adversely affecting populations of several important fishery species. Marine mammals can be adversely effected by commercial or sport fishing (competition for food supply and accidental by-catch), ingestion of plastics and other human generated wastes in the marine environment, loss of food supply, and encroachment on resting and breeding areas. Unfortunately, assessing the health of marine populations is difficult due to the costs associated with assessment and insufficient knowledge about the marine environment and its inhabitants. The data bases and vital statistics regarding many marine species are often limited or non-existent.

Looking Forward

There are indications of improving conditions in some aspects of the offshore ocean zone, and ecosystem degradation in others. The most current biological surveys indicate that blue, fin, and humpback whale populations have grown markedly in recent years. The number of gray whales migrating between Mexico and the Bering Sea along the California coast appears to represent those estimated to have existed prior to the onset of commercial whaling activities in the Pacific Ocean. Consequently, the gray whale has recently been taken off the federal endangered species list. Associated with this resurgence of marine mammal populations has been a corresponding growth in the west coast "whale-watching" industry.

Although conditions for some species are improving, a study released by the Scripps Institution of Oceanography (Scripps) indicates that warming trends in Southern California waters are resulting in substantial zooplankton kills off the west coast. These water temperature increases may be robbing surface water of valuable nutrients needed to sustain the zooplankton populations. The phenomenon, which is cited as occurring over the last 10-30 years, is having a detrimental impact on higher level marine resources, such as fishery and seabird populations, that previously existed off the coast. (Roemmich and McGowan 1995). Long term monitoring of ocean conditions and fisheries is critical for determining the health of ocean resources.

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) has completed 45 years of sampling physical, chemical, and biological resources within the California Current off Southern California. In 1994, CalCOFI published the second of two atlases which summarize the distribution and abundance of fish larvae collected on CalCOFI surveys from 1951 to 1984. CalCOFI is working with scientists from the National Oceanic and Atmospheric Administration, Scripps, California Department of Fish and Game, Mexican government, and others on a wide variety of research and monitoring efforts.

CONCLUSION

California's four resource zones are dynamic and interdependent, forming one of the biologically richest ecosystems in the world. Management of the ocean's resources must take into consideration this interdependence and recognize that impacts generated in one resource zone may ultimately affect resources in another zone.

The ocean ecosystem also contributes substantially to the economic health of the State. However, numerous human activities are exerting increasing pressures on the marine environment, which can negatively affect California's precious ocean resources and the commercially valuable industries they support. California's coast has supported human activities since early settlements were established, but environmental impacts have increased as growing human populations compete for land, port and harbor facilities, recreational areas, fishing grounds, mineral resources, and reserves for natural resource protection. Now, more than ever, it is important that California's ocean management program assess the ecological and economic impacts of activities on California's ocean ecosystem, and to determine the most

effective and efficient methods for addressing those impacts. Success in this initiative will be highly dependent on the ability of the State to focus attention on resolving major policy issues in cooperation with all levels of government, the public, and the private sector.

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May 2, 2006

Dwight E. Sanders
California State Lands Commission
100 Howe Avenue, Suite 100-South
Sacramento, CA 95825

Comment on revised DEIR: Cabrillo Port intake and impacts on ichthyoplankton in the Santa Barbara Channel

To the commission:

I would like to point out that there are two major problems with the ichthyoplankton impact study:

1. While the actual intake is relatively close to shore and very shallow, the "quadrat" chosen for comparison is very large, and extends far offshore (note where the intake sits in the quadrat). The larger area chosen for comparison, the effect will be proportionally smaller (imagine what the numbers would look like if one used the volume of the entire California Current as a denominator). Percentage mortality is therefore misleading; it is much clearer to simply state the amount of water that will be directly affected by the operations (nearly four billion gallons per year).
2. More seriously, the CalCOFI samples are from water that is deeper and further offshore on average than the water being used by the project. Since plankton densities generally increase as samples are taken shallower and nearer shore, the CalCOFI numbers for density would be an underestimate of the density at the site. Note that their source water body depth went down to 210m. Note that in the consultation records, Dr. Peter Raimondi pointed out this problem and suggested that it needed to be discussed. I found no such discussion in the document, only a statement that "it has been determined that data from all stations...is relevant to determining Project entrainment impacts." (p 11).

These observations raise serious concerns for the validity of the DEIR.

Sincerely,

A handwritten signature in cursive script that reads 'Robert R. Warner'.

Robert R. Warner
Professor of Marine Biology

CURRICULUM VITAE

ROBERT R. WARNER

INTERESTS: Behavioral ecology; the interaction of behavior and life history; population ecology, particularly in coral reef fishes.

PERSONAL: Born October 28, 1946; U. S. Citizen

PROFESSIONAL EXPERIENCE:

- 1964 - 67 Analytical chemist, Atlantic Richfield Oil Co., Wilmington, CA (summers).
- 1970 Research histologist, U.S. Bureau of Commercial Fisheries
- 1973 Programmer and Field Assistant, Marine Ecological Consultants, Solana Beach, CA

UNIVERSITY EMPLOYMENT:

- 1973 Instructor, San Diego City College, CA
- 1975-81 Assistant Professor of Marine Biology, Dept. of Biological Sciences, UC Santa Barbara.
- 1982-85 Associate Professor of Marine Biology, Dept. of Biological Sciences, UC Santa Barbara.
- 1985 Professor of Marine Biology, Dept. of Biological Sciences, UC Santa Barbara.
- 1990-95 Vice-Chair, Dept. of Biological Sciences, UC Santa Barbara.
- 1995 Acting Chair, Dept. of Biological Sciences, UCSB
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- | | | | |
|-------|------|--------------------|---|
| A.B. | 1968 | Vertebrate Zoology | UC Berkeley |
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ROBERT R. WARNER

HONORS/AWARDS/SPECIAL APPOINTMENTS:

- 1964 Kraft Award, UC Berkeley
- 1965-68 Academic Scholarships, UC Berkeley
- 1968 Phi Beta Kappa, UC Berkeley
- 1968 Graduated with distinction in general scholarship and in the honors zoology program.
- 1971 Academic scholarship, Scripps Institution of Oceanography
- 1973-75 Postdoctoral fellowship, Smithsonian Tropical Research Institute
- 1982 Plenary Speaker: Fourth European Ichthyology Congress, Hamburg
- 1983 Plenary Speaker: International Ethological Congress, Brisbane
- 1986 C.I.M.A.S. Distinguished Professor, University of Miami
- 1988 Main Speaker: Symposium on Recruitment, Sixth Intl. Coral Reef Congress, Townsville, Aust.
- 1990 Darwin lecturer, University of Kentucky
- 1990 Lawrence Distinguished Professor, SUNY Stony Brook
- 1991 Plenary Speaker: International Ethological Congress, Kyoto
- 1992 Tester Distinguished Professor, University of Hawaii
- 1996 Plenary Speaker: Eighth International Coral Reef Congress, Panama
- 1996-2000 Editorial Board, *Behavioral Ecology*
- 1997 Plenary Speaker, Coastal and Reef Processes: Strategic Development ARC Symposium, James Cook University, Australia
- 1998 Plenary Speaker, Annual International Symposium, The Fisheries Society of the British Isles
- 1998 OUEVRE Visioning Committee for NSF Biological Oceanography
- 1998 Councillor, Society for the Study of Evolution
- 1999 NCEAS Sabbatical Fellowship
- 1999 Marine Reserves Scientific Advisory Panel, Channel Islands National Marine Sanctuary
- 2000-05 Editorial Board, *Journal of Ethology*
- 2001 Distinguished Marine Scientist – Oregon State University
- 2002-05 Research Chair, Channel Islands National Marine Sanctuary Advisory Council
- 2005 Plenary speaker, 7th Indo-Pacific Fish Conference, Tapei

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INVITED LECTURES:

- 1975 Seminars: Smithsonian Tropical Research Institute
 Yale University
 Guelph University
 UC Berkeley
 UC Santa Barbara
 UC Los Angeles
- 1976 Seminars: Scripps Institution of Oceanography
 Calif. State University, San Francisco
 California Academy of Sciences
 Symposium: Tropical Biology, UCLA
- 1977 Seminars: Smithsonian Tropical Research Institute
- 1978 Seminars: Cornell University
 McGill University
 UC Davis
 Symposium: Sociobiology, AAAS, Washington, D.C.
- 1979 Seminars: University of Utah
 University of Arizona
 Arizona State University
 UC Santa Cruz
- 1980 Seminars: UC Riverside
 UC Irvine
 Scripps Institution of Oceanography
- 1981 Seminars: University of Nevada
 Oregon State University
 University of Alberta, Canada
- 1982 Seminars: Max Planck Institute, Seewiesen, F.R.G.
 University of Freiburg, F.R.G.
 University of Groningen, Netherlands
 Symposium: International Ethological Congress, Oxford
 Main Plenary Speaker: Fourth European Ichthyology Congress, Hamburg
- 1983 Seminars: Scripps Institution of Oceanography
 University of Utah
 Plenary Speaker: International Ethological Congress, Brisbane
- 1984 Symposium: Collias Honorary, UCLA

ROBERT R. WARNER

INVITED LECTURES: (Cont'd)

- 1985 Seminars: Ohio State University
 University of Kentucky
 University of New Mexico
 University of California, Santa Barbara
 S.T.A.R.E.S.O., Calvi, Corsica
 University of British Columbia
 Simon Fraser University
 Princeton University
 Symposia: Coral Reef Congress, Tahiti
 Indo-Pacific Fish Congress, Tokyo
- 1986 Seminars: C.I.M.A.S. Visiting Professor, University of Miami
 Symposium: Sex Determination, University of Colorado
- 1987 Seminars: Scripps Institution of Oceanography
 Symposium: Ethology and Evolutionary Ecology of Fishes
- 1988 Seminars: McGill University
 Laval University
 West Indies Laboratory, St. Croix
 Main Speaker: Symposium on Recruitment, Sixth Intl. Coral Reef
 Congress, Townsville, Aust.
- 1989 Seminars: University of North Dakota
 University of Minnesota
- 1990 Darwin Lecturer: University of Kentucky
 Lawrence Distinguished Visiting Professor, SUNY Stony Brook
 Seminars: U.C. Davis
 University of Georgia
 Scripps Institution of Oceanography
 Oxford University
 Cambridge University
 Uppsala University
- 1991 Seminars: Imperial College, Silwood Park
 University of Berne
 University of Zurich
 University of Basel
 Brown University
 Plenary Speaker: International Ethological Congress, Kyoto
- 1992 Seminars: Northern Arizona University
 University of the Virgin Islands
 Oregon State University
 Tester Distinguished Professor, University of Hawaii

ROBERT R. WARNER

INVITED LECTURES: (Cont'd)

- 1993 Symposium: Sexual Selection in Lower Vertebrates (ASIH, Austin)
 Seminars: University of New Hampshire
 Pepperdine University
 Cuesta College
 University of Arizona
- 1994 Seminars: University of North Carolina
 University of Southern California
- 1995 Seminars: Uppsala University, Sweden
 SUNY Buffalo
- 1996 Seminars Calif. State University, Northridge
 Scripps Institution of Oceanography (Rosenblatt symposium)
 Eastern Michigan University
 Michigan State University
 Plenary Speaker, Eighth International Coral Reef Congress, Panama
- 1997 Seminars Scripps Institution of Oceanography, UCSD
 Department of Psychology, UCSB
 Evolutionary Behavior and Social Science Seminar, UCSB
 University of Padova, Italy
 National Center for Ecological Analysis and Synthesis
 Plenary Speaker, Coastal and Reef Processes: Strategic Development
 ARC Symposium, James Cook University, Australia
- 1998 Seminars Florida State University
 University of Florida
 Cornell University
 Humbolt State University
 Workshop OEUVRE (Future of Marine Ecology) NSF, Keystone, CO.
 Working Group Marine Protected Areas (National Center for Ecological
 Analysis and Synthesis)
 Working Group Connectivity in Marine Populations (NSF, Santa Barbara,
 CA)
 Symposium: Marine Protected Areas (NOAA and Mote Marine Laboratory,
 Sarasota, Florida)
 Plenary Speaker, Annual International Symposium, The Fisheries Society of
 the British Isles

ROBERT R. WARNER

INVITED LECTURES: (Cont'd)

1999	Seminars	Oregon State University National Center for Ecological Analysis and Synthesis University of California, Riverside University of California, Santa Cruz
	Working Group	Marine Protected Areas (National Center for Ecological Analysis and Synthesis)
	Working Group	Long-term Marine Records (National Center for Ecological Analysis and Synthesis)
	Working Group	Open vs. closed marine populations (National Center for Ecological Analysis and Synthesis) – convenor
2000	Seminars	National Center for Ecological Analysis and Synthesis Pacific Marine Fisheries Council Channel Islands Marine Reserves Working Group Pacific Marine Conservation Council Sustainable Seas Expedition Coordinating Group Communication Partnership for Science and the Sea
	Working Group	Marine Protected Areas (National Center for Ecological Analysis and Synthesis)
	Working Group	Long-term Marine Records (National Center for Ecological Analysis and Synthesis)
	Working Group	Open vs. closed marine populations (National Center for Ecological Analysis and Synthesis) – convenor
2001	Seminars	Scripps Institution of Oceanography Oregon State University North Carolina State University
	Speaker	Consultative Group on Biological Diversity Annual Meeting
	Symposium	American Association for the Advancement of Science The Theory of Marine Reserves
	Invited speaker	Second workshop on North American Marine Protected Areas
	Interlocutor	Marine Conservation Biology Symposium on Zoning in the EEZ
2002	Seminars	Scripps Institution of Oceanography
	Speaker	COMPASS Symposium on Marine Reserves US House of Representatives: House Ocean Caucus US House of Representatives: Committee on Resources California Fish and Game Commission California World Ocean Conference Chancellor's breakfast group
	Working Group	Marine Protected Areas II (National Center for Ecological Analysis and Synthesis)

ROBERT R. WARNER

INVITED LECTURES: (Cont'd)

2003	Seminars	University of Connecticut College of the Atlantic
	Symposia	American Association for the Advancement of Science Coastal Marine Ecology Evolution of Sex and Gender
	Workshop	NSF: Connectivity in marine populations
	Working Group	Marine Protected Areas II (National Center for Ecological Analysis and Synthesis)
2004	Seminars	Hopkins Marine Station, Stanford Florida State University University of Miami
	Working Groups	Marine Protected Areas II (National Center for Ecological Analysis and Synthesis) Land-sea connections (National Center for Ecological Analysis and Synthesis) NOAA National Marine Protected Areas Center – Integration of Marine Protected Areas and Fishery Science and Management
	Symposia	International Coral Reef Congress, Okinawa – Connectivity in Marine Populations International Coral Reef Congress Satellite Meeting – Sex Allocation (Keynote speaker) Friday Harbor Laboratory - Ecosystem-based Management for Resilience

ROBERT R. WARNER

EXTRAMURAL GRANTS:

National Geographic Society	Sex change in coral reef fishes	1976 \$6,500
National Science Foundation (with A. Ebeling)	Continued analysis of kelp-bed fish communities	1976-78 \$138,000
National Science Foundation	Using sex change to test hypotheses in life history and and behavior	1978-81 \$80,000
National Science Foundation	Behavioral and population ecology of coral reef fishes	1981-84 \$141,000
European Ichthyology Congress	Travel Grant	1982 \$650
International Ethological Congress	Travel Grant	1983 \$745
National Science Foundation	Behavioral and population ecology of coral reef fishes	1984-87 \$210,000
National Science Foundation	Selection for male traits and female preference in a coral reef fish	1987-90 \$252,000
National Science Foundation	Research experience for undergraduates in coral reef ecology	1989 \$8,000
National Science Foundation	Mating site determination and catastrophic change	1990 \$5,300
National Science Foundation	Mating group size and sex allocation	1991 \$7,500
NOAA	Recruitment limitation vs. density dependence in reef fish populations	1991-92 \$64,000
International Ethological Congress	Travel Grant	1991 \$475
National Science Foundation	Mate choice in the bicolor damselfish, <i>Stegastes partitus</i> .	1991-92 \$8770

ROBERT R. WARNER

EXTRAMURAL GRANTS (Cont'd):

National Science Foundation	Protandrous fishes as tests of sex allocation theory	1991-92 \$8500
National Science Foundation	Behavioral and population ecology of coral reef fishes	1992-95 \$200,000
National Science Foundation	Graduate Minority Fellowship Supplement to above grant	1993-96 \$62,000
National Science Foundation	Mating dynamics in a pelagically-spawning coral reef fish	1992-95 \$155,000
National Science Foundation	REU Supplement to the above grant	1994-95 \$5000
National Science Foundation	Gamete allocation in benthically-spawning reef-fishes	1994-96 \$15,000
International Conservation Society	Sources of recruitment in coral reef fishes	1995-96 \$2500
National Science Foundation	Interactions between reproductive strategies and mating system structure	1995-99 \$265,000
W. M. Keck Foundation	Coastal Research Initiative: New links between ocean physics and marine population dynamics (5 co-PIs)	1996-99 \$650,000
National Science Foundation	SGER: Using ICP-MS to detect sources of recruitment in marine fishes	1996-98 \$50,000
International Society for Reef Studies	Travel grant	1996 \$810
National Science Foundation	The effect of intra- and intersexual conflict on patterns of mating behavior (with S. Henson)	1997-99 \$10,000
Packard Foundation	Partnership for Interdisciplinary Studies of Coastal Oceans (8 co-PIs)	1999-04 \$17,800,000

ROBERT R. WARNER

EXTRAMURAL GRANTS (Cont'd):

Environmental Defense Fund	Can we design marine reserves to export larval fishes to surrounding populations? (with G. E. Forrester)	1999-01 \$15,000
National Science Foundation	NCEAS Sabbatical Fellowship: Open vs. Closed Marine Populations: Synthesis and Analysis of the Evidence	1999-00 \$70,000
California Sea Grant	Linking early fish growth and transport to circulation using otolith microstructure and microchemistry (with M. Love)	2001-02 \$95,000
UCOP	Larval Pathways and Population Connectivity in Nearshore Marine Organisms (with S. Swearer)	2002-03 \$500,000
Center for Marine Conservation	Larval retention and Population Connectivity in the Galapagos Marine Reserve (with B. Ruttenberg)	2002-03 \$14,000
Packard Foundation	Communicating the Science of Marine Reserves (with J. Lubchenco, S. Gaines, S. Aíramé, and B. Simler)	2002-2003 \$241,796
National Science Foundation	Coupled Physical-Human System Biocomplexity: Flow, Fish and Fishing: Disparate Scales of Process Make Nearshore Fishery Management a Difficult Task (5 co-Pis)	2003-2008 \$1,600,000
Packard Foundation	Partnership for Interdisciplinary Studies of Coastal Oceans (12 co-PIs)	2003-04 \$1,290,000

ROBERT R. WARNER

EXTRAMURAL GRANTS (Cont'd):

California Sea Grant	Use of natural tags in <i>Loligo opalescens</i> paralarvae to trace dispersal history (with J. Caselle)	2003-04 \$10,000
Australian Research Council	Discovery Grant: Do larval fish leave the reef to avoid parasites? (with A. Grutter, M. McCormick, A. Kuris)	2004-07 \$330,000
National Science Foundation	Collaborative Research: Tracking Invertebrate Larval Trajectories (with D. Zacherl, S. Gaines)	2004-2007 \$268,000
National Park Service	Larval retention, larval exchange and population connectivity in the Hawaiian Islands (with S. Hamilton, B. Ruttenberg)	2004-2005 \$20,000
Packard Foundation and Moore Foundation	Partnership for Interdisciplinary Studies of Coastal Oceans (12 co-PIs)	2004-09 \$24,500,000

ROBERT R. WARNER

PUBLICATIONS:

1970 McGowan, J. A., M. A. Barnett, R. E. Davis, R. R. Warner, and M. E. Silver. The ecology and oceanography of sewer outfalls. S.I.O. ref. no. 70-18.

1973 Perrin, W. F., R. R. Warner, C. H. Fiscus, and D. B. Holts. Stomach contents of porpoise (*Stenella* spp.) and Yellowfin Tuna (*Thunnus albacares*) in mixed-species aggregations. Fish. Bull. 71:1077-1092.

1975 Warner, R. R. The reproductive biology of the protogynous hermaphrodite *Pimelometopon pulchrum* (Pisces: Labridae). Fish. Bul. 73:262-283.

Warner, R. R. The adaptive significance of sequential hermaphroditism in animals. Amer. Natur. 109:61-84.

Warner, R. R., D. R. Robertson, and E. G. Leigh, Jr. Sex change and sexual selection. Science 190:633-638.

1976 Leigh, E. G. Jr., E. Charnov, and R. R. Warner. Sex ratio, sex change, and natural selection. Proc. Nat. Acad. Sci. 73:3656-3660.

1977 Warner, R. R. and I. F. Downs. Comparative life histories: growth vs. reproduction in normal males and sex-changing hermaphrodites of the striped parrotfish, *Scarus croicensis*. Proc. Third Int. Coral Reef Symposium 275-281.

1978 McCosker, J. E., L. Taylor, and R. R. Warner. Ichthyological studies in the Galapagos. Noticias de Galapagos 27:13-15.

Warner, R. R. Patterns of sex and coloration in the Galapagos wrasses *Bodianus eclancheri* and *Pimelometopon darwini*. Noticias de Galapagos 27:16-18.

Warner, R. R. and D. R. Robertson. Sexual patterns in the labroid fishes of the Western Caribbean. I. The Wrasses (Labridae). Smithsonian Contributions to Zoology 254:1-27.

Robertson, D. R. and R. R. Warner. Sexual patterns in the labroid fishes of the Western Caribbean. II. The Parrotfishes (Scaridae). Smithsonian Contributions to Zoology 255:1-26.

Warner, R. R. The evolution of hermaphroditism and unisexuality in aquatic and terrestrial vertebrates. Pages 77-101 in E. Reese and F. J. Lighter, eds. Contrasts in behavior. Wiley-Interscience, N.Y.

Warner, R. Sexual-asexual evolutionary equilibrium? Amer. Natur. 112(987):960-962.

ROBERT R. WARNER

PUBLICATIONS: (Cont'd)

- 1980 Warner, R. The coevolution of behavioral and life history characteristics. Pages 151-188 in G. W. Barlow and J. Silverberg, eds. *Sociobiology: Beyond Nature - Nurture?* Westview Press, Boulder, Colorado.
- Warner, R. R. and S. G. Hoffman. Local population size as a determinant of mating system and sexual composition in two tropical marine fishes (*Thalassoma* spp.) *Evolution* 34(3):508-518.
- Warner, R. R. and S. G. Hoffman. Population density and the economics of territorial defense in a coral reef fish. *Ecology* 61(4):772-780.
- 1981 Chesson, P. and R. R. Warner. Environmental variability promotes coexistence in lottery competitive systems. *Amer. Natur.* 117:923-943.
- Hoffman, S. G. and R. R. Warner. The cost of experience and the outogamy of males under contest competition for mates. *Amer. Zoo.* 21:948. (Abstract)
- 1982 Warner, R. R. Mating systems, sex change and sexual demography in the rainbow wrasse, *Thalassoma lucasanum*. *Copeia* 1982(3):653-661.
- Warner, R. R. and R. K. Harlan. Sperm competition and sperm storage as determinants of sexual dimorphism in the dwarf surfperch, *Micrometrus minimus*. *Evol.* 36(1):44-45.
- Warner, R.R.. Metamorphosis. *Science* '82 3:42-46.
- 1983 Warner, R. R. Review of *Marine Ecology* by J. S. Levinton. *Quart. Rev. Biol.* 58:106-107.
- 1984 Warner, R. R. Deferred reproduction as a response to sexual selection in a coral reef fish: a test of the life historical consequences. *Evolution* 38:148-162.
- Warner, R. R. Mating systems and hermaphroditism in coral reef fish. *Amer. Sci.* 72:128-136.
- Warner, R. R. Population density, mating territoriality, and sex change in coral reef fishes. *Natl. Geographic Society Research Reports* 17:909-912.
- Warner, R. R. Recent developments in the ecology of tropical reef fishes. *Arch. Fisch Wiss.* 35:43-53.
- 1985 Warner, R. R. and P. L. Chesson. Coexistence mediated by environmental variability: a field guide to the storage effect. *Amer. Natur.* 125:769-787.

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PUBLICATIONS: (Cont'd)

- 1985 Hoffman, S. G., M. P. Schildhauer, and R. R. Warner. The costs of changing sex and the ontogeny of males under contest competition for mates. *Evolution* 39(4):915-927.

Warner, R. R. and P. Lejeune. Sex change limited by paternal care: a test using four Mediterranean labrid fishes, genus *Symphodus*. *Mar. Biol.* 87:89-99.

Warner, R. R. Alternative mating behaviors in a coral reef fish: a life-history analysis. *Proc. Fifth Int. Coral Reef Congress* 4:145-150.

- 1986 Warner, R. R. The environmental correlates of female infidelity in a coral reef fish. In: *Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes*. (T. Uyeno, R. Arai, T. Taniuchi, and K. Matsuura, eds.) pp. 803-810. Ichthyological Society of Japan, Tokyo.

- 1987 Warner, R.R. Female choice of sites versus males in a coral reef fish, *Thalassoma bifasciatum*. *Anim. Behav.* 35:1470-1478.

- 1988 Warner, R.R. Boys will be boys - or girls. *Natural History* 97:76-77.

Warner, R.R. Sex change in fishes: hypotheses, evidence, and objections. *Env. Biol. Fishes* 22:81-90.

Warner, R.R. Sex change and the size advantage model. *Trends in Ecology and Evolution* 3:133-136.

Warner, R.R. Traditionality of mating-site preferences in a coral-reef fish. *Nature* 335:719-721.

Warner, R.R. and T.P. Hughes. The population dynamics of reef fishes. *Proc. Sixth Int. Coral Reef Congress* 1:149-155.

- 1989 van den Berghe, E.P. and R.R. Warner. The effects of mating system on male mate choice in a coral reef fish. *Behavioral Ecology and Sociobiology* 24:409-415.

Schultz, E.T. and R.R. Warner. Phenotypic plasticity in life-history traits of female *Thalassoma bifasciatum* (Pisces:Labridae) I. Manipulations of social structure in tests for adaptive shifts of life history allocations. *Evolution* 43:1497-1506.

R.R. Warner Inapplicability of the size advantage model to coral reef fishes - reply. *Trends in Ecology and Evolution* 4:272-273.

ROBERT R. WARNER

PUBLICATIONS: (Cont'd)

- 1989 van den Berghe, E.P., F. Wernerus and R.R. Warner. Female choice and the mating cost of peripheral males. *Animal Behaviour* 38:875-884.
- 1990 Warner, R.R. Resource assessment vs. traditionality in mating site determination. *American Naturalist* 135: 205-217
- Schultz, E.T. and R.R. Warner. Phenotypic plasticity in life-history traits of female *Thalassoma bifasciatum* (Pisces: Labridae) II. Correlation of fecundity and growth rate in comparative studies. *Environmental Biology of Fishes* 30: 333-344
- Warner, R. R. Male vs. female influences on mating site determination. *Animal Behaviour* 39: 540-548.
- 1991 Warner, R. R. The use of phenotypic plasticity in coral reef fishes as tests of theory in evolutionary ecology. pp 387-398. In: *The Ecology of Coral Reef Fishes* (P. Sale, ed.). Academic Press
- Schultz, E.T., L.G. Clifton and R.R. Warner. Constraints versus tactics: the adaptive significance of breeding schedule variation in a marine fish (Embiotocidae: *Micrometrus minimus*). *American Naturalist* 138: 1408-1430.
- Warner, R. R., and S. Swearer. Social control of sex change in the bluehead wrasse, *Thalassoma bifasciatum* (Pisces: Labridae). *Biological Bulletin* 181: 199-201.
- Knapp, R. A., and R. R. Warner. Male parental care and female choice in the bicolor damselfish *Stegastes partitus*: bigger is not always better. *Animal Behaviour* 41: 747-756.
- 1992 Warner, R. R., and E. T. Schultz. Sexual selection and male characteristics in the bluehead wrasse, *Thalassoma bifasciatum* : mating site acquisition, mating site defense, and female choice. *Evolution* 46: 1421-1442.
- Petersen, C. W., R. R. Warner, S. Cohen, H. C Hess, and A. T. Sewell. Variation in pelagic fertilization success: implications for production estimates, mate choice, and the spatial and temporal distribution of spawning. *Ecology* 73: 391-401.
- 1995 Warner, R. R., F. Wernerus, P. Lejeune, and E. P. van den Berghe. Dynamics of female choice for parental care in a species where care is facultative. *Behavioral Ecology* 6: 73-81

ROBERT R. WARNER

PUBLICATIONS: (Cont'd)

- 1995 Dunham, M. L., R. R. Warner, and J. Lawson. The dynamics of territory acquisition: a model of two coexisting strategies. *Theoretical Population Biology* 47: 347-364.
- Warner, R. R. Large mating aggregations and daily long-distance spawning migrations in the bluehead wrasse, *Thalassoma bifasciatum*. *Environmental Biology of Fishes* 44: 337-345
- Warner, R. R., A. Marconato, D. Y. Shapiro, and C. W. Petersen. Sexual conflict: males with highest mating success convey the lowest fertilization benefits to females. *Proc. Roy. Soc. B* 262:135-139.
- 1996 Warner, R. R., D. E. Fitch, and J. Standish. Social control of sex change in the shelf limpet, *Crepidula norrisiarum*: size-specific responses to local group composition. *J. Exp. Marine Biol. Ecol.* 204: 155-167
- Godwin, J., R. Sawby, R. R. Warner, D. Crews, and M. S. Grober. Adult sex reversal is associated with changes in AVT mRNA expression in the preoptic area. *Society for Neurosciences Abstracts* 22: 298.
- Godwin, J., D. Crews, and R. R. Warner. Behavioural sex change in the absence of gonads in a coral-reef fish. *Proceedings of the Royal Society B* 263: 1683-1688.
- Caselle, J. E., and R. R. Warner. Variability in recruitment in coral reef fishes: importance of habitat at large and small spatial scales. *Ecology* 77: 2488-2504
- 1997 Barrett, H. C., and R. R. Warner. Female influences on male reproductive success. Pp 334-350 In: *Feminism and Evolutionary Biology* (P. Gowaty, ed.), Chapman and Hall, New York.
- Warner, R. R. Evolutionary ecology: how to reconcile pelagic dispersal with local adaptation. *Coral Reefs* 16S: s115-128. (Also appeared in *Proc. 8th International Coral Reef Congress* 1: 75-79)
- Warner, R. R. Sperm allocation in coral reef fishes. *BioScience* 47: 561-564.
- Henson, S., and R. R. Warner. Male and female alternative reproductive behaviors in fishes: a new approach using intersexual dynamics. *Annual Review of Ecology and Systematics* 28: 571-592
- Marconato, A., D. Y. Shapiro, C. W. Petersen, R. R. Warner, and T. Yoshikawa. Methodological analysis of fertilization rate in the bluehead wrasse, *Thalassoma bifasciatum* : pair versus group spawns. *Marine Ecology Progress Series* 161:61-70.

ROBERT R. WARNER

PUBLICATIONS: (Cont'd)

- 1997 Henson, S A., and R. R. Warner. The effect of conflict within and between the sexes on reproductive behaviour. p. 234 In Taborsky, M. and B. Taborsky (Eds.). *Advances in Ethology*, 32. Contributions to the XXV International Ethological Conference. vii+323p. Blackwell Wissenschafts-Verlag GmbH: Berlin, Germany.
- 1998 Petersen, C. W., and R. R. Warner. Sperm competition and sexual selection in fishes. Pp 435-463 In: *Sperm competition and sexual selection* (T. R. Birkhead and A. P. Møller, eds.) Academic Press.
- Wooninck, L., J. E. Strassman, D. C. Queller, R. Fleischer, and R. R. Warner. Characterization of hypervariable microsatellite markers in the bluehead wrasse, *Thalassoma bifasciatum*. *Molecular Ecology* 7:1613-1614.
- Warner, R. R. The role of extreme iteroparity and risk-avoidance in the evolution of mating systems. *Journal of Fish Biology* 53(Supp A):82-93.
- 1999 S. E. Swearer, J. E. Caselle, D. W. Lea, and R. R. Warner. Larval retention and recruitment in an island population of a coral-reef fish. *Nature* 402: 799-802.
- Alonzo, S. H., and R. R. Warner. A trade-off generated by sexual conflict: Mediterranean wrasse males refuse present mates to increase future success. *Behavioral Ecology* 10:105-111.
- Luttbeg, B., and R. R. Warner. Flexible reproductive decision making: environments that favor using prior experience to make decisions. *Behavioral Ecology* 10: 666-674
- 2000 Alonzo, S. H. and R. R. Warner. Female choice, conflict between the sexes, and the evolution of male alternative reproductive behaviours. *Evolutionary Ecology Research* 2: 149-170
- Alonzo, S. H. and R. R. Warner. Dynamic games and field experiments examining intra- and inter-sexual conflict: explaining counter-intuitive mating behavior in a Mediterranean wrasse, *Symphodus ocellatus*. *Behavioral Ecology* 11: 56-70
- Warner, R. R., S. E. Swearer, and J. E. Caselle. Larval accumulation and retention: implications for the design of marine reserves and essential fish habitat. *Bulletin of Marine Science* 66: 821-830
- Warner, R. R., and L. M. Dill. Courtship displays and coloration as indicators of safety rather than of male quality: the safety assurance hypothesis. *Behavioral Ecology* 11: 444-451

ROBERT R. WARNER

PUBLICATIONS: (Cont'd)

- 2000 Godwin, J., R. Sawby, R. R. Warner, D. Crews, and M. S. Grober. Hypothalamic arginine vasotocin mRNA abundance variation across the sexes and within sex change in a coral reef fish. *Brain Behavior And Evolution* 55: 77-84.
- Wooninck, L., R. R. Warner, and R. Fleischer. Relative fitness components measured with competitive PCR. *Molecular Ecology* 9: 1409-1414
- Alonzo, S. H. and R. R. Warner. Allocation to mate-guarding or increased sperm production in a Mediterranean wrasse. *American Naturalist* 156:266-275
- 2001 C. W. Petersen, R. R. Warner, D. Y. Shapiro, and A. Marconato. Components of fertilization success in the bluehead wrasse, *Thalassoma bifasciatum*. *Behavioral Ecology* 12: 237-245.
- C. M. Roberts, B. Halpern, S. R. Palumbi, and R. R. Warner. Designing marine reserve networks: why small, isolated protected areas are not enough. *Conservation Biology in Practice* 2: 11 – 17.
- J. B. C. Jackson, M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. Bradbury, R. Cooke, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293: 629 - 638.
- Warner, R. R., M. Carr, C. Syms, S. Morgan, P. Dayton, and S. Aïramé. Analysis and Evaluation of the Draft Marine Protected Area Network for California State Waters. Technical Report for the Natural Resources Defense Council and the World Wildlife Fund. San Francisco, California.
- 2002 Halpern, B., and R. R. Warner. Marine reserves have rapid and lasting effects. *Ecology Letters* 5: 361-366.
- Warner, R. R. Synthesis: Environment, mating systems, and life-history allocations in the bluehead wrasse. Pp. 227-244 In: *Model Systems in Behavioral Ecology* (L. Dugatkin, ed.) Princeton University Press, Princeton, N.J.
- Petersen, C. W., and R. R. Warner. The reproductive behavior of coral reef fishes in an ecological context. Pp. 103-118 In: *Coral Reef Fishes: New Insights into their Ecology* (Peter F. Sale, ed.) Academic Press, San Diego
- Warner, R. R. and R. K. Cowen. Local retention of production in marine populations: evidence, mechanisms, and consequences. *Bulletin of Marine Science* 70: 245-249.

ROBERT R. WARNER

PUBLICATIONS: (Cont'd)

- 2002 Swearer, S. E., J. S. Shima, M. E. Hellberg, S. R. Thorrold, G. P. Jones, D. R. Robertson, S. G. Morgan, K. A. Selkoe, G. M. Ruiz, and R. R. Warner. Evidence of self-recruitment in demersal marine populations. *Bulletin of Marine Science* 70: 251-271.

Thorrold, S. R., G. P. Jones, M. E. Hellberg, R. S. Burton, S. E. Swearer, J. E. Neigel, S. G. Morgan, and R. R. Warner. Quantifying larval retention and connectivity in marine populations with artificial and natural markers. *Bulletin of Marine Science* 70: 291-308.

Strathmann, R. R., T. P. Hughes, A. M. Kuris, K. C. Lindeman, S. G. Morgan, J. M. Pandolfi, and R. R. Warner. Evolution of self-recruitment and its consequences for marine populations. *Bulletin of Marine Science* 70:377-396.

Halpern, B., R. R. Warner, and S. Gaines. Letter to the editor in response to "Measuring effects of marine reserves on fisheries: the dilemmas of experimental programs." *MPA News* 4:5

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- 2003 Palumbi, S. R., and R. R. Warner. Why gobies are like hobbits. *Science* 299:51-52.

Zacherl, D. C., P. H. Manríquez, G. Paradis, R. W. Day, J. C. Castilla, R. R. Warner, D. W. Lea, and S.D. Gaines. Trace elemental fingerprinting of gastropod statoliths to study larval dispersal trajectories. *Marine Ecology Progress Series*. 248: 297-303

Carr, M., J. Neigel, J. Estes, S. Andelman, R. R. Warner, and J. Largier. Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. *Ecological Applications* 13 (Supp.): S90-S107.

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